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RESEARCH ARTICLE

Predators balance consequences of climate-change-induced habitat shifts for range-shifting and resident species

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Abstract

1. While many species distributions are shifting poleward or up in elevation in response to a changing climate, others are shifting their habitats along localized gradients in environmental conditions as abiotic conditions become more stressful. Whether species are moving across regional or local environmental gradients in response to climate change, range-shifting species become embedded in established communities of competitors and predators. The consequences of these shifts for both resident and shifting species are often unknown, as it can be difficult to isolate the effects of multiple species interactions.
2. Using a model system of insects in high-elevation ponds in the Rocky Mountains of Colorado, we sought to disentangle the effects of predation and intraguild interactions on the survival and development of a semi-permanent pond resident caddisfly *Limnephilus externus* and the habitat-shifting caddis *Asynarchus nigriculus* that is being forced into semi-permanent ponds as temporary ponds dry too quickly to complete development.
3. We conducted a manipulative in-situ pond cage experiment in which *L. externus* and *A. nigriculus* caddisfly larvae in single-species treatments and together were exposed to the presence/absence of predatory *Dytiscus* diving beetle larvae. This approach allowed us to isolate the effects of intraguild interactions and predation on the survival and development of both the resident and habitat-shifting species.
4. We found that intraguild interactions had strong negative effects on the resident and habitat-shifting species. Intraguild interactions reduced the survival of the resident *L. externus* and increased the variation in survival of the shifting *A. nigriculus*. However, *Dytiscus* predators reduced these negative effects, stabilizing the community by increasing *L. externus* survival and reducing variation in *A. nigriculus* survival. We also found that intraguild interactions reduced *L. externus* biomass but resulted in increased *A. nigriculus* development. *A. nigriculus* development was also increased by predation.
5. Our results show that strong intraguild interactions between resident and shifting species are likely to have negative consequences for both species. However, the presence of predators reduces these negative consequences of the habitat shift on both the resident and the shifting.

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KEYWORDS
competition, predation, range-shift, species interactions, trichoptera, variability

1 | INTRODUCTION

Localized environmental gradients play important roles in maintaining biodiversity and structuring ecological communities. Often times, this occurs as a consequence of evolutionary trade-offs where adaptations to conditions (both abiotic and biotic) at one end of the gradient decrease performance at the other (Kneitel & Chase, 2004; Lubchenco, 1980; Welborn et al., 1996). A classic example is in the rocky intertidal where competition in the abiotically comfortable low tide zone forces some species to adapt to the desiccation stress of the high tide zone (Connell, 1961). However, climate change is altering environmental gradients which is likely to have significant consequences for the processes structuring ecological communities (Martin, 2001; Parmesan, 2006). Moreover, while species range shifts across elevational and latitudinal gradients are a well-documented response to increased abiotic pressures induced by climate change (Chen et al., 2011; Parmesan & Yohe, 2003), species may also alter their habitat use along localized environmental gradients and seek refuge in areas they may have traditionally been rare in or excluded from by abiotic stress, biotic interactions or both (Davies et al., 2006; Harley, 2011; Kordas et al., 2015).

Studies of range or habitat shifts in response to climate change have largely focused on relationships between the shifting species and abiotic variables or pairwise interactions with competitors, but the community consequences of habitat shifts are less understood (e.g. Lenoir & Svenning, 2015; Shepard, Wissinger, & Greig, 2021). When a species moves into a habitat it was previously absent from or rare in, it becomes embedded within a suite of new, or previously rare, interspecific interactions including competition and predation. The outcome of any such shift will depend on the balance of these interactions (Lurgi et al., 2012). For example, resident predators may play important roles in altering competitive or other intraguild interactions between resident and shifting species of lower trophic levels (Chase et al., 2002; Chesson & Kuang, 2008; Jones et al., 2020). Disentangling the roles that these various, simultaneous, interactions play in the outcomes of shifts in habitat use should be one of the primary objectives of studies seeking to understand the outcomes of species responses to climate change. Here we experimentally investigate the consequences of predation and intraguild interactions for resident and habitat-shifting species.

Understanding the impact of species interactions on the outcomes of habitat shifts also requires examining multiple life-history variables. Demographic compensation, where decreases in fitness due to changes in one demographic variable are offset by increases in another, is common population response to changing environments (Villellas et al., 2015). For example, increased growth rates have been shown to offset survival rates in tundra plants (Doak & Morris, 2010). Indeed, examining multiple life-history parameters can be critical in disentangling the relative importance of abiotic and biotic variables for determining the outcomes of habitat shifts (Shepard, Wissinger, & Greig, 2021).

One habitat where climate-change-induced alterations to localized abiotic gradients are likely to be particularly important is high-elevation ponds and wetlands. These habitats are generally considered to have low diversity (de Mendoza & Catalan, 2010; Fjellheim et al., 2009; Füreder et al., 2006) so even modest changes in community structure may have outsized impacts on diversity, stability and function (Rooney & McCann, 2012; Tilman, 1999; Wissinger et al., 2016). Hydroperiod—the duration for which a pond holds surface water—is a critical environmental gradient in alpine habitats (Welborn et al., 1996; Wissinger et al., 1999, 2003, 2006) and climate change is expected to shorten hydroperiod as spring snowmelt timing advances, summer temperatures increase and precipitation becomes less predictable (Barnett et al., 2005; Tuytens et al., 2014). As a result, species that inhabit temporary ponds may be forced to use ponds with longer hydroperiods if temporary ponds dry faster than species' development rates can tolerate (Lund et al., 2016; Sim et al., 2013). These shifting organisms will then be interacting with a different, and potentially more diverse, assemblage of competitors and predators than what is typical of more temporary habitats (Welborn et al., 1996; Wissinger et al., 2009).

To understand the potential biotic consequences of this predicted change in habitat use, we conducted an in-situ cage experiment in semi-permanent ponds at the Mexican Cut Nature Preserve in Colorado, USA in which we examined the interaction between *Asynarchus. nigriculus* (Banks, 1908), *Limnephilus externus* (Hagen, 1861) and a top predator, *Dytiscus* diving beetle larva. *A. nigriculus* is common in temporary ponds (those that dry every year) and occasionally is found in semi-permanent basins as well (Wissinger et al., 2003, 2006). We anticipate, however, that as hydroperiods shorten with climate change *A. nigriculus* will be forced to shift its habitat and rely on semi-permanent ponds (those that only occasionally dry) to sustain its population, thus shifting its habitat. *L. externus* is commonly found in semi-permanent ponds, as are *Dytiscus* beetle larvae (Wissinger et al., 1999).

Previous studies of this system have shown that the aggressive foraging traits of *A. nigriculus* that underlie its success in temporary ponds reduces the survival of *L. externus* when the two compete for resources (Wissinger, Whiteman, et al., 1999). Indeed, both species consume detritus as their primary food source (Wissinger et al., 2018) but *A. nigriculus* is also known to engage in intraguild predation on confamilial species including *L. externus* (Wissinger et al., 1996). Therefore, we would expect *A. nigriculus* reduce the survival of *L. externus* when the two species are together. However, we anticipate that higher-order predators would modify this interaction by removing the more aggressive species, in this case *A. nigriculus*, and allow

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for a more stable coexistence (Chase et al., 2002; Leibold, 1996; Paine, 1966). Indeed, *Dytiscus* predators in microcosms select *A. nigriculus* larvae over *L. externus* larvae because they are more active and poorly defended (Wissinger et al., 2006). Thus, in the more biologically realistic scenario with both competitors and predators present, we hypothesize that *A. nigriculus* may have reduced survival while *L. externus* maintains a relatively high population. To ensure we did not miss any effects of demographic compensation, we also quantified the responses of development and body mass in these caddisflies in response to predation and intraguild interactions. We hypothesized that these variables would follow similar patterns to survival because behaviours that promote development and growth in these caddisflies also make them more vulnerable to adverse effects of competitors and predators (Wissinger et al., 2006; Wissinger, Whiteman, et al., 1999).

2 | MATERIALS AND METHODS

2.1 | Study system

Our research was conducted at the Mexican Cut Nature Preserve (MCNP) in the Rocky Mountains of Colorado, USA (39.030, −107.064). This site contains a collection of more than 60 subalpine ponds and wetlands of varying hydroperiod (Wissinger, Bohonak, et al., 1999). Limnephilid caddisflies are the biomass-dominant macrodetritivores in the ponds at the MCNP with five species distributed across permanently inundated ponds, semi-permanent ponds that dry in autumn of years with low precipitation and temporary ponds that dry in summer every year (Wissinger et al., 2003; Wissinger, Whiteman, et al., 1999). One species, *A. nigriculus* is the dominant temporary pond species but may also be found, in semi-permanent ponds, though typically in lower abundances (Wissinger et al., 2003). This very aggressive and active species develops rapidly (first instar to adult in <45 days) but is vulnerable to predators found in permanent and semi-permanent ponds (Wissinger et al., 2003, 2006; Wissinger, Whiteman, et al., 1999). In contrast, *L. externus*, which is dominant in permanent and semi-permanent ponds, is well defended against predators but its slow development excludes it from temporary habitats (Wissinger et al., 2003, 2006). Additionally, *L. externus* has a Holarctic distribution (Morse, 2021; Rasmussen & Morse, 2020) and is broadly distributed across the regional elevation gradient (2,200–3,400 m a.s.l.) while *A. nigriculus* is largely restricted to subalpine elevations (3,200–3,500 m a.s.l.) and is only found in a small subset of the United States (Morse, 2021; Rasmussen & Morse, 2020).

Despite the differences in the breadths of their distributions, both of these species can co-occur in semi-permanent habitats (Wissinger et al., 2003). However, as hydroperiod shortens with climate change (Tuytens et al., 2014), we expect *A. nigriculus* may not be able to rely on temporary ponds (Lund et al., 2016) and habitat use in semi-permanent ponds may play a larger role in the maintenance of the meta-population, especially in particularly dry years. Indeed, drying events resulting in cohort failures of *A. nigriculus* in temporary ponds have been becoming more frequent at this site in recent years (Lund et al., 2016) and semi-permanent ponds provide refuge habitats from which recolonization of temporary ponds can occur.

2.2 | Cage experiment

We investigated whether the interaction between *A. nigriculus* and *L. externus* is modified by *Dytiscus* predatory diving beetle larva by conducting a field experiment with cages set within ponds at the MCNP (39.030–107.064). Cages (50 × 50 × 50 cm, 1-mm mesh walls) were set within in the shallow littoral zone of five semi-permanent ponds that dry in the late summer of warm years with little precipitation but remain inundated during wetter years (Wissinger, Bohonak, et al., 1999). Each pond received six cages, each with a different treatment: *L. externus* on its own, *A. nigriculus* on its own, *L. externus* and *A. nigriculus* together, with those three treatments crossed by the presence and absence of predation pressure by *Dytiscus* diving beetle predators. Thus, the treatments that had both species of caddisfly included intraguild predation and competition which we describe hereafter as intraguild interactions.

To avoid artificially inflating predation rates by enclosing a mobile predator in a confined arena with high densities of prey (Bergström & Englund, 2002; Englund, 1997; Petersen & Englund, 2005), we only exposed caddisflies to predators for 1 hr every other day. Furthermore, we did not begin putting predators into the appropriate cages until 1 week after the experiment began to mimic the phenological lag between the *Dytiscus* predators and the caddisflies (Greig & Wissinger, 2010; Wissinger et al., 2006). Each cage received 99.90 ± 0.24 g of *Carex* sedge detritus as a basal resource for the caddisflies and densities were held constant at 160 individuals/m^2 resulting in 40 individuals per cage. Thus, in the intraguild interaction treatments, we used a substitutive design with 20 individuals of each species (Shepard, Wissinger, & Greig, 2021). The densities we used in this experiment fall within the natural observed range in semi-permanent ponds for *L. externus* (3–393 m^2) and temporary ponds for *A. nigriculus* (1–193 m^2). Our use of a substitutive design matches patterns of replacement we have observed in these ponds previously (S. A. Wissinger, unpubl. data). Furthermore, substitutive designs tend to make it more difficult to detect effects of intraguild interactions thus making our approach to a more conservative one in this regard (Kiær et al., 2013). Initial instar ratios were kept consistent across the treatments. *A. nigriculus* was kept at 15% 4th instars and 85% 5th instars and *L. externus* was started at 15% 2nd instars and 85% 3rd instars. These ratios reflect what was observed in natural surveys of the ponds taken at the beginning of the experiment and reflect the developmental advantage of *A. nigriculus* over *L. externus* that facilitates intraguild predation (Greig & Wissinger, 2010). Cages were fitted with emergence traps on the lids to capture any adult caddis that emerged during the experiment. Emergence traps were checked every other day during the course of the experiment.

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The cage experiment ended after 19 days (1 August–19 August 2019) when a majority of *A. nigriculus* had begun to pupate. At this point, we removed the cages from the ponds and collected remaining caddisfly larvae and pupae from each cage. We also collected and froze the remaining detritus in each cage which was subsequently inspected in the laboratory to detect any caddisflies that may have been missed in the field. The total number of caddisflies from each cage were enumerated and their development stage identified. Pupae were divided into two groups: early and late based on whether developing wings were visible. No special ethical approvals were required for this research.

2.3 | Analysis

2.3.1 | Individual survival

We used binomial general linear mixed models to determine whether intraguild interactions, predation or the interaction of both influenced the survival of both *L. externus* and *A. nigriculus*. The interaction term was included to test whether there were any non-additive effects of having both intraguild interactions and predation occurring at the same time. We ran separate models for each species. In both models, we included random effects for pond and cage within to account for variation across space. We used Type II Wald chi-squared tests to determine the significance of the intraguild interactions, predation and intraguild interactions by predation interaction terms in both models. Finally, we used Tukey post-hoc tests to examine pairwise differences in the four treatment survival estimates (intraguild interactions present/absent × predation present/absent) for both models. Mixed-effects models were created using the LME4 package (Bates et al., 2015), the Wald chi-square tests were performed using the CAR package (Fox & Weisburg, 2019) and the Tukey tests were performed using the MULTCOMP package (Horthon et al., 2008) in R version 3.6.1 (R Core Team, 2019).

We also examined the effects of predation, intraguild interactions and their interaction on the variation in individual survival for both *L. externus* and *A. nigriculus*. To do this, we examined the ratio of observed variation in individual survival to the expected variation therein for each treatment in the above two models. If observed variation is higher than expected variation, then survival rates are highly variable or stochastic within a given treatment. If observed variation is lower than expected variation, then survival rates are largely consistent within a given treatment. Expected variation for a binomial variable with rate p is equal to $p(1 - p)$. We therefore calculated the expected variation in individual survival by multiplying the treatment-specific survival estimates by one minus themselves. We calculated actual variation using the residuals from each treatment, then calculated the ratio of observed to expected variation. We used bootstrapping ($n = 1{,}000$) to generate standard errors around these ratios. We then conducted Tukey post-hoc tests to examine pairwise differences in the four-treatment observed/expected variation ratios for both models, using the actual residual data degrees of freedom (594).

2.3.2 | Development

We also examined the effect of intraguild interactions, predation and their interaction on the development of the caddisflies. To do this, we used ordinal regression to estimate the probability that an individual *A. nigriculus* would be in a given development stage for a given treatment. In other words, we used this model to predict how development would be influenced by the presence of intraguild interactions and/or predators. This model also had an interaction term to determine whether there were any non-additive effects on development when both predation and intraguild interactions were present. To account for variation across space, we also included a term for cage in the model. Our model and predictions were generated using the ORDINAL package (Christensen, 2015) in R version 3.6.1 (R Core Team, 2019). We assessed the parallel lines assumption using a Brant test using the BRANT package (Schlegel & Steenbergen, 2020) in R version 3.6.1 (R Core Team, 2019) which indicated that the assumption was met. We did not conduct development stage analysis on *L. externus* because all *L. externus* individuals at the same developmental stage (5th instars) at the end of the experiment. Term significance was determined using a Wald test from the CAR package (Fox & Weisburg, 2019).

2.3.3 | Mass

Lastly, we examined the final mass of the individual larvae in the cages. Mass data were collected by removing caddisfly larvae from their cases and then drying the bodies in an oven at 60°C for 48 hr. We then measured the individual dry mass of up to 10 individuals from each cage to the nearest 0.001 mg with a Cahn C-31 microbalance (Thermo Scientific). We only analysed larval mass for *L. externus* because most of the *A. nigriculus* had pupated or emerged as adults resulting in too small a sample size for analysis on late instar body mass. The anatomical and physiological changes that occur between pupation and adulthood mean that late instar larva, pupal and adult body masses are not comparable. Examination of *L. externus* body mass data showed that it had a strong right skew, which we reduced with a square root transformation. We used general linear mixed-effects models to determine the effect of intraguild interactions, predation and their interaction on *L. externus* larval mass. As in the other two models, the interaction term was used to test for non-additive effects of the combination of predation and intraguild interactions. These models also had a nested random effect of cage within pond to account for variation across space. We conducted a Type II Wald *F* test to determine the significance of each term in the model. Models were created using the LME4 package (Bates et al., 2015) and Wald tests were done using the CAR package (Fox & Weisburg, 2019) in R version 3.6.1 (R Core Team, 2019).

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3 | RESULTS

3.1 | Survival

Broadly, our analyses indicate that predation reduces the effects of intraguild interactions on either the mean or variation in survival. Whether these effects of intraguild interactions and predation affect the mean, or the variation, depends on species identity. The resident species, *L. externus*, showed changes in its mean survival based on treatment (Figure 1a) while the shifting species, *A. nigriculus*, showed changes in the variation around survival based on treatment (Figure 1d).

Limnephilus externus had the highest survival in the absence of both intraguild interactions and predators (Figure 1a). Intraguild interactions with *A. nigriculus* reduced *L. externus* survival to 45% compared to 80% survival in single species *L. externus* treatments (Figure 1a; Table 1). However, the effect of these interactions was only significantly different from all other treatments when predators were absent. When predators and intraguild interactions were present, *L. externus* survival was 53% which was not significantly different from treatments with only *L. externus* or *L. externus* and intraguild interactions (significant intraguild interaction × predation interaction, Table 1; Figure 1a). Predation on its own had similar effects on *L. externus* survival whether intraguild interactions were present or not and, on its own was not significant (Table 1; Figure 1a). Together these results indicate intraguild interactions have a stronger influence on *L externus* survival than predation.

In contrast, our models indicated that *A. nigiriculus* had consistently low survival (19%–30%) across all treatments (Figure 1b) and there were no significant effects of intraguild interactions, predation or their interaction on their survival (Table 1). While seemingly low, the overall observed rate of mortality for *A. nigriculus* in our experiment matched that seen in natural ponds both with and without predators (Figure S1).

The variation in survival within treatments for both species showed a much different pattern than mean survival. *L. externus* had relatively consistent variation across all treatments, and observed variation was largely in line with expected variation with no significant differences between treatments (Figure 1c). However, we did see significant effects of intraguild interactions and predation on the variation in *A. nigriculus* survival. Specifically, in the absence of both intraguild interactions and predators *A. nigriculus* survival showed lower variation than expected (Figure 1d). However, the presence of intraguild interactions increased the variation in survival, with a ratio of expected to observed variation greater than 1. When predators were added to this interaction, the observed variation decreased back below zero with the treatment where *A. nigriculus* was on its own being the only one with lower variation. However, due to large amounts of variation in the estimate for the intraguild interaction only treatment, the difference between intraguild interaction treatments with and without intraguild interactions was not significant. On their own, predators reduced variation in *A. nigriculus* survival but not as much as the combination of predators and intraguild interactions (Figure 1d).

3.2 | Development

Estimates of the probabilities that *A. nigriculus* would develop to a given stage within the timeframe of our experiment showed that reaching the late pupal stage (i.e. wings developing) was the most common outcome in all treatments (Figure 2). Development was the

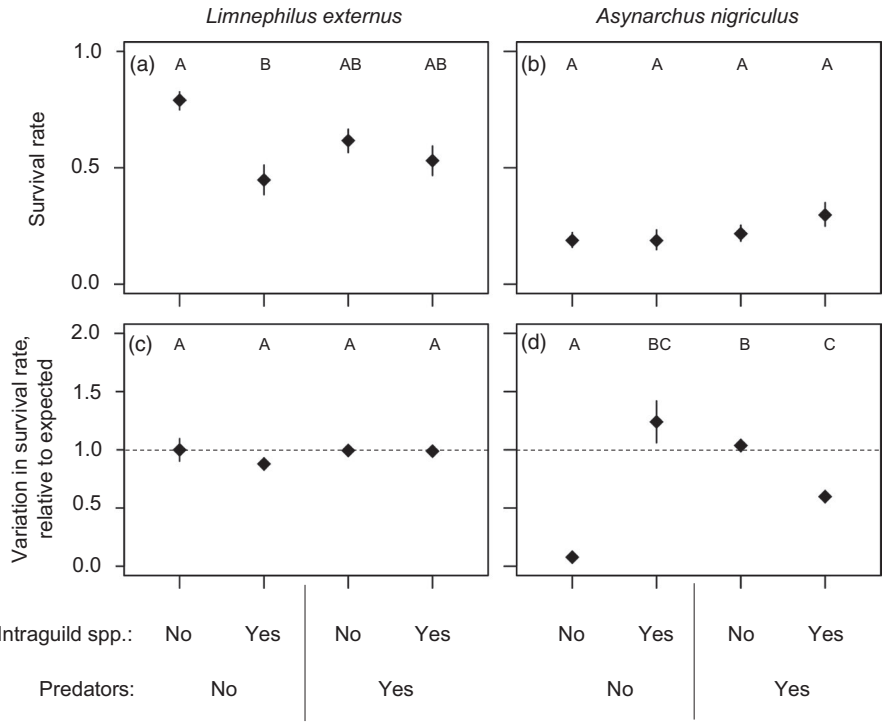


FIGURE 1 Survival rate of (a) *Limnephilus externus* and (b) *Asynarchus nigriculus* in the presence and absence of intraguild interactions and predators in high alpine ponds in Colorado, USA. The lower panels show the observed versus expected variation in survival (see methods) for (c) *L. externus* and (d) *A. nigriculus* in the presence and absence of intraguild interactions and/or predators in high alpine ponds in the Elk Mountains, Colorado, USA. Points above the dashed line show greater than expected variation while points below show less variation than expected. Error bars show standard errors. Letters indicate results of Tukey Honest Significant Difference Tests (see Section 2)

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TABLE 1 Type II Wald χ^2 tests on two binomial mixed-effects models estimating individual survival of two species of caddisfly under different intraguild interaction and predation treatments in high alpine ponds

Species	Term	χ^2	*df*	*p*	*SD*
Limnephilus externus	Intraguild Ints.	14.652	1	<0.001	
	Predation	2.048	1	0.152	
	Intraguild Ints. × Predation	6.090	1	0.014	
	Pond				0.080
	Pond:Cage				0.342
Asynarchus nigriculus	Intraguild Ints.	0.966	1	0.326	
	Predation	2.271	1	0.132	
	Intraguild Ints. × Predation	0.829	1	0.363	
	Pond				9.53×10^{-7}
	Pond:Cage				0.237

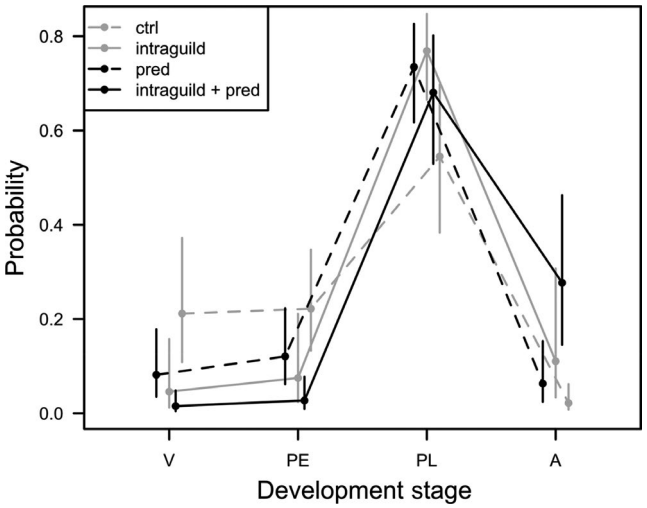


FIGURE 2 Probability of a surviving individual *Asynarchus nigriculus* being either fifth instar larva, early pupa, late pupa or adult after 19 days of exposure to intraguild interactions (intraguild), predators (pred), both (intraguild + pred), or neither (ctrl) in high-elevation ponds in the Elk Mountains of Colorado, USA. Error bars represent 95% confidence intervals

fastest in treatments with both intraguild interactions and predators (Figure 2). The intraguild interaction by predation interaction term was not significant indicating no non-additive effects of the two treatments together (Table 2). However, in the absence of intraguild interactions or predators, individual *A. nigriculus* were more likely to be found in earlier instars than in any other treatment after the same amount of time (Figure 2). Moreover, the probability of a surviving individual developing to adulthood was the highest when both predators and intraguild interactions were present. Intraguild interactions and predation, but not their interaction, had significant effects on the development of *A. nigriculus* (Table 2). In other words, development was slowest when *A. nigriculus* was on its own, intermediate when either predators or intraguild interactions were present, and fastest when both intraguild interactions and predators were present (Figure 2). No development analysis was conducted for *L. externus* because all individuals recovered at the end of the experiment were in the same development stage.

TABLE 2 Model output from ordinal regression on the effects of intraguild interactions, predation, and their interaction on the development of *Asynarchus nigriculus* in semi-permanent ponds in the Elk Mountains of Colorado, USA. *p*-values obtained from Wald tests

Variable	Estimate	*SE*	*z*	*p*
Cage	0.009	0.016	0.609	0.543
Intraguild Ints.	1.706	0.688	2.478	0.013
Predation	1.101	0.465	2.468	0.018
Intraguild Ints. × Predation	0.030	0.838	0.035	0.972

3.3 | Mass

Our linear mixed-effects model showed a strong, negative effect of intraguild interactions on *L. externus* larval mass. *L. externus* individuals from treatments with *A. nigriculus* were, on average, 40% smaller than those in treatments without intraguild interactions (Table 3; Figure 3). However, there was no significant effect of predation on body mass, or intraguild interaction × predation interaction term (Table 3; Figure 3).

4 | DISCUSSION

Our study provides strong empirical evidence that the outcome of climate-induced shifts in habitat use along environmental gradients is shaped by interspecific interactions with resident intraguild species and predators in the recipient community. *L. externus*, the resident species in this experiment, largely responded in ways we predicted, with intraguild interactions reducing survival and predators weakening that effect. This was not the case for *A. nigriculus*, the shifting species in our study, which showed no differences in survival between treatments. By exploring the mechanisms driving these observed responses, we can hypothesize the broader consequences for the future of these high alpine pond systems. Moreover, we may be able to develop a generalizable understanding of how communities may respond to future environmental

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TABLE 3 Type II Wald *F* test on a linear mixed-effects model, plus random effect standard deviations, examining the effects of predation and intraguild interactions on *Limnephilus externus* mass in high-elevation ponds

Term	*F*	*df*	*p*	*SD*
Intraguild Ints.	45.994	1	<0.001	
Predation	0.162	1	0.695	
Intraguild Ints. × Predation	0.419	1	0.530	
Pond				0.243
Pond:Cage				0.094

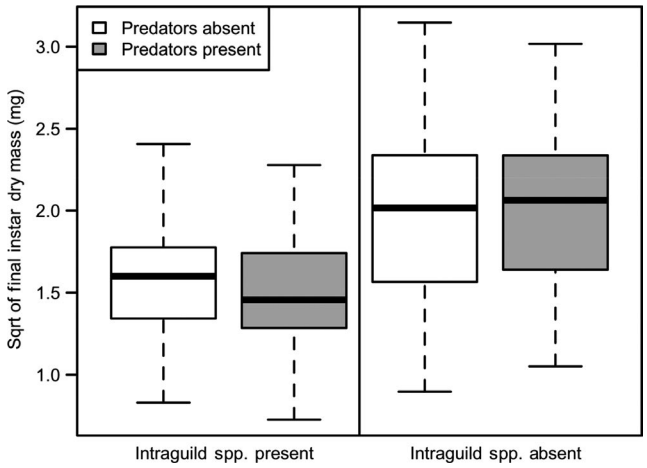


FIGURE 3 The square root of the dry mass of fifth instar *Limnephilus externus* alone and in the presence of an intraguild species, predators and both in high alpine ponds in the Elk Mountains of Colorado, USA

changes and what is necessary to predict the outcomes of such changes.

Proportional survival was highest for *L. externus* when individuals interacted only with conspecifics and the lowest in the presence of the aggressive competitor/intraguild predator, *A. nigriculus*. These results indicate that reductions in *L. externus* survival from intraguild predation and other aggressive behaviours by *A. nigriculus* (e.g. Wissinger et al., 2004) likely exceed the density-dependent declines in survival and performance observed in single species *L. externus* assemblages (Klemmer et al., 2012). Predation on its own did not have a significant effect on *L. externus* survival which is not surprising given the robust case and risk sensitive behaviour of *L. externus* substantially reduces its vulnerability to predators (Wissinger et al., 2006). However, the combination of predation and intraguild interactions significantly decreased the proportional *L. externus* survival, albeit less than when predators were not included in the intraguild interaction treatment. This outcome could be because predators reduce *A. nigriculus* survival, thereby releasing *L. externus* from intraguild predation and other antagonistic interactions (as in Chase et al., 2002). However, we observed consistently low *A. nigriculus* survival across all treatments and no significant effects of *Dytiscus* predation on *A. nigriculus* survival. This would indicate that the role of predation in this regard is likely more indirect.

We can better understand the mechanism through which predation reduces the effect of *A. nigriculus* on *L. externus* survival by examining other demographic data. In the presence of predators, we saw increased development of *A. nigiriculus*. Given that *A. nigriculus* individuals do not accelerate their development in response to predators (Greig & Wissinger, 2010), we hypothesize that predators may remove smaller, more slowly developing *A. nigriculus* individuals from the population generating a demographic structure that would appear to show an increased development rate. Moreover, if slower-to-develop individuals are selectively removed from the population early by predation, *L. externus* will be exposed to fewer intraguild predators as the remaining, later instar, *A. nigriculus* individuals quickly begin to pupate and cease being intraguild predators. Nevertheless, *L. externus* at the beginning of the experiment is still probably experiencing some antagonistic interactions from the larger *A. nigriculus* before they pupated, as evidenced by the observed decrease in *L. externus* survival in the presence of both predators and intraguild interactions compared to *L. externus* on its own. Indeed, this intraguild predation likely was a mechanism behind the more advanced development in *A. nigriculus* we observed in the presence of the intraguild species as *A. nigriculus* develops more quickly if it has a protein-rich diet consistent with intraguild prey (Wissinger, Steinmetz, et al., 2004). Thus, the advanced development of *A. nigriculus* we observed in the presence of predators and intraguild species is likely an additive response of predators removing the more slowly developing individuals and intraguild predation allowing those that survived to develop more quickly.

While *A. nigriculus* had a markedly negative effect on *L. externus* survival, the overall fitness ramifications of a potential shift by *A. nigriculus* to semi-permanent ponds do not stop there. Intraguild interactions with *A. nigriculus* significantly decreased the 5th instar body mass of *L. externus* regardless of the presence of predators. *L. externus* is risk sensitive in the presence of predators and aggressive competitors, often retreating into its case and remain still when threatened (Wissinger et al., 2006). This behaviour decreases foraging time and resource acquisition (Wissinger et al., 2004). Thus, the constant pressure of *A. nigriculus* in the treatments with intraguild interactions might have reduced the amount of time *L. externus* spent foraging, with costs to larval mass. Larval body mass has a well-known predictor of adult body mass (Day et al., 2002) and fecundity in insects, especially non-feeding females (Honěk, 1993; Jannot et al., 2007). Thus, should *A. nigriculus* shift its habitat to interact with *L. externus* more frequently, we may see an overall decrease in the fecundity of the *L. externus* population at the MCNP. Indeed, assuming that the relationship between body mass and fecundity is the same for both of these confamilial species, a 40% decrease in body mass such as we observed would decrease individual fecundity by 33% (Wissinger, Steinmetz, et al., 2004). However, knowing for certain whether these decreases in mass would ultimately impact *L. externus* population size, even in the presence of predators, would require quantifying differences in total egg production (e.g. Jannot

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et al., 2008) and whether egg production influences recruitment and subsequent population size (Hildrew et al., 2004).

Regardless, it is clear *L. externus* is likely to suffer some negative consequences if *A. nigriculus* abundance increases in semi-permanent ponds in response to climate change. This may have important ramifications on the rest of the community as *L. externus* is the most common and biomass-dominant caddisfly species in the system (Wissinger, Bohonak, et al., 1999). Decreases in its local abundance may allow other range-shifting species, such as those from lower elevations, to establish a greater foothold in the region (Shepard, Wissinger, & Greig, 2021). There may also be important consequences for ecosystem-level processes such as detritus breakdown and nutrient dynamics in these ponds as *L. externus* is the single greatest detritus processer in the oligotrophic system where we conducted our study (Klemmer et al., 2012; Wissinger et al., 2018).

In contrast to the resident species, the shifting species, *A. nigriculus* did not respond as we predicted. Proportional survival was low and nearly uniform across all treatments with no significant effects of predation or intraguild interactions. This suggests that *A. nigriculus* shows strong density-dependent morality driven by space and resource availability. It would be easy to assume that these results are the product of a context-independent, internally driven process and that densities are regulated by intraspecific interactions such as cannibalism (Wissinger, Steinmetz, et al., 2004). Yet, our data showing treatment effects on both development stage and the variation around proportional survival indicate that there are likely different mechanisms removing individuals from the population in different scenarios. Indeed, mortality rates of *A. nigriculus* in cages with and without *Dytiscus* predators are nearly the same as those in ponds with and without *Dytiscus* (Figure S1). As discussed above, *Dytiscus* predators were likely important for removing slow to develop individuals from the population. Further support for this notion is seen in the amount of variation in the estimates of proportional survival which were nearly equal to lower than model estimates when predators were present, indicating consistent, predictable removal of individuals from the population.

Asynarchus nigriculus populations in the presence of *L. externus* without predators showed much higher variation in survival than expected by the model. Incidental cannibalism may be responsible for this outcome. As described by Wissinger et al. (1996) and Wissinger, Eldermire, et al. (2004), *A. nigriculus* exhibit a mob-like 'feeding frenzy' behaviour in instances of intraguild predation, or cannibalism, in which individuals are attracted to an *A. nigriculus* that is consuming prey. The aggressive encounters that ensue result in injury of conspecifics and the subsequent expulsion of body fluids into the water by the wounded individual triggers further cannibalism (Wissinger, Eldermire, et al., 2004). Thus, it is possible that intraguild predation events may be associated with instances of secondary cannibalism that increases variability in *A. nigriculus* survival among replicates. Moreover, individuals that gain a protein boost from cannibalism may become larger than their conspecifics (Wissinger, Steinmetz, et al., 2004) which could further promote cannibalism as it has been shown to be size-structured (Wissinger et al., 1996). In sum, we hypothesize that low-frequency events that trigger a positive feedback loop may generate the irregularities in survival seen across replicates with intraguild interactions.

Together, our observations of the response of *A. nigriculus* to the intraguild interactions and predators of semi-permanent ponds show that this species has the potential to exploit and thrive in these habitats should the need arise. Indeed, the increased development shows that *A. nigriculus* will likely develop in time to emerge from semi-permanent ponds, even as future climate scenarios predict these ponds may dry more often or more quickly (Tuytens et al., 2014). However, the overall low observed survival rate would indicate that additional perturbations to the system might cause this species to lose its foothold in these habitats since smaller populations are more susceptible to localized extinctions (O'Grady et al., 2004). The performance of *A. nigriculus* in semi-permanent habitats may be critically important since semi-permanent ponds may become source populations and their preferred, temporary ponds, may become sink populations under future climate predictions (Lund et al., 2016; Sim et al., 2013). Under this scenario, continued persistence of this species will depend on whether population density and recruitment in semi-permanent habitats can compensate for losses in the regional metapopulation as temporary ponds become uninhabitable. Indeed, local scale metapopulation dynamics can play important roles in determining species persistence as climate change drives shifts in habitat use (Fordham et al., 2013; Wilson et al., 2010). Future work examining whether population dynamics in these semi-permanent ponds can offset losses in temporary ponds will be fruitful in this regard.

On a broader level, our study reveals that climate-change-induced localized habitat shifts may result in the destabilization of ecological communities. The interaction between *L. externus* and *A. nigriculus* had significant consequences for *L. externus* survival and growth, which can be a hallmark of strong interactions (Berlow et al., 2004). Strong interactions in ecological communities tend to be destabilizing (Gellner & McCann, 2016). The increasing regularity of such a strong interaction, especially one that involves a foundational species in the system may have broad consequences for community persistence (Landi et al., 2018). Furthermore, this intraguild interaction resulted in high variation in *A. nigriculus* survival, which at the population level is also an important indicator of instability, particularly in a changing climate (Halley et al., 2018). Instability in the potentially shifting species can decrease establishment success in new refuge habitats if currently preferred habitat becomes inhospitable due to climate change as unstable populations are less likely to persist through time (Lande, 1993). However, our results indicate *Dytiscus* predators reduce this instability by weakening the interaction between *A. nigriculus* and *L. externus* while reducing the amount of variation in *A. nigriculus* survival. This reinforces the importance of maintaining, intact ecological communities with high order predators when promoting the resilience of ecological systems to habitat shifts in response to climate change (Wang et al., 2020).

Indeed, the beneficial role of the *Dytiscus* predation we observed is perhaps unsurprising given the keystone role of

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predators for maintaining biodiversity (Chase et al., 2002) and stabilizing ecological communities (Rooney & McCann, 2012) is well understood. However, the role of predation in determining the outcomes of climate-induced habitat shifts has largely been overlooked. While there has been some consideration of the role that shifting predators may play on community structure and stability (Bartley et al., 2019), little evidence exists demonstrating how resident consumers alter the outcomes of shifts involving organisms from lower trophic levels. Our findings demonstrate that the members of resident communities and their interactions with each other and with shifting species can be critically important for determining how communities will respond to shifts in habitat use as the climate changes.

5 | CONCLUSIONS

Here we have shown that some species may respond in predictable ways to localized habitat shifts while others might not. However, using a deep knowledge of the organisms' life histories we can readily explain the mechanisms likely responsible for the observed patterns even if they were beyond what we predicted initially, especially when multiple life-history variables were considered. Predators were particularly important in reducing the strength of intraguild interactions between these species and reducing variation in the survival of the potentially shifting species which, together, has important implications for the stability of this community in the future. Ultimately, this kind of information is important for predicting how communities will respond to current and future climate change by helping us identify which species may need special protections to ensure their survival in the new communities that emerge. Future studies examining larger components of the food web will be fruitful in this regard.

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CONFLICT OF INTEREST

The authors claim no conflicts of interest, financial or otherwise, regarding the research presented in this manuscript.

AUTHORS' CONTRIBUTIONS

I.D.S., H.S.G. and S.A.W. conceived and conducted the experiment; I.D.S. and Z.T.W. analysed the data; I.D.S. lead the manuscript writing with H.S.G. and Z.T.W. All authors contributed critically to the drafts and approved the final manuscript.

DATA AVAILABILITY STATEMENT

All data presented in this manuscript are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.r7sqv9sd3 (Shepard, Wissinger, Wood, et al., 2021).

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